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Seasonal and diurnal increases in energy stores in migratory warblers at an autumn stopover site along the Asian-Australasian flyway

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Keywords:

migration, stopover, refuelling, flight range, songbird, East Asia, *Phylloscopus*

Abstract:

In contrast to the rapidly growing knowledge on migratory routes, wintering grounds, and timing of annual life cycle events, the knowledge with respect to how songbirds refuel at stopover sites along the Asian-Australasian flyway has increased only slowly, despite that migrant birds along this flyway show declining trends. We analysed the amount and variation of energy stores between species, variation of energy stores within the day and within the season, and estimated flight ranges of ten closely related warbler species (genera *Acrocephalus*, *Arundinax*, *Locustella* and *Phylloscopus*), captured at a stopover site in the Russian Far East during autumn migration. We found significant differences in species' energy stores, with Pallas's Leaf Warbler *Phylloscopus proregulus* having by far the highest. All species increased their energy stores within the day, and eight species increased their energy stores within the season. Individuals with the highest estimated flight ranges were able to cover a distance of 470 km during one nocturnal flight bout, which would lead to a minimum of nine stopovers before the birds reach their wintering grounds. We assume that a combination of multiple factors shapes the variation in energy stores between the species. We discuss the potential of exploiting different habitats, differences in refuelling strategy according to the distribution of species-specific refuelling habitats along the migratory route, and the potential to exploit a variety of food resources. This study is the first to provide information on energy stores, refuelling strategies and flight ranges for a set of closely related songbird species migrating along the Asian-Australasian flyway.

Deutsche Zusammenfassung

Der Kenntnisstand zu den Zugwegen, den Winterquartieren und der zeitlichen Organisation des Jahreszyklus ziehender Singvogelarten hat sich in den letzten Jahren stark verbessert. Weitaus weniger ist über die Fettdeposition und die Rastökologie bekannt. Dies gilt insbesondere für Singvogelarten, welche entlang der Ostasiatischen Route in ihre Winterquartiere ziehen. Hier vergleichen wir die Energiereserven von zehn verschiedenen Arten aus den Gattungen *Acrocephalus*, *Arundinax*, *Locustella* und *Phylloscopus* an einem Zwischenrastplatz im Fernen Osten Russlands während des Herbstzuges. Dabei analysieren wir Unterschiede

zwischen den Arten und im Verlauf des Tages und der Saison. Wir konnten signifikante zwischenartliche Unterschiede in den Energiereserven finden, wobei Goldhähnchen-Laubsänger *Phylloscopus proregulus* die höchsten Reserven aufwiesen. Alle Arten zeigten eine Zunahme im Tagesverlauf, und bei acht Arten konnten wir eine signifikante Zunahme im Laufe der Herbstsaison feststellen. Basierend auf den beobachteten Energiereserven konnten wir maximale Flugreichweiten berechnen, wobei die fettesten Individuen bis zu 470km in einer Nacht zurücklegen könnten. Damit müssten die Vögel mindestens neun Mal rasten, um ihre Winterquartiere in Südostasien zu erreichen. Wahrscheinlich ist eine Vielzahl von Faktoren für die zwischenartlichen Unterschiede in den Energiereserven relevant. Zum Einen sind die Habitate und die verfügbare Nahrung in unserem Untersuchungsgebiet vermutlich von verschiedener Qualität für verschiedene Arten. Zum anderen könnten die Arten unterschiedliche Zugstrategien aufweisen, je nach Verfügbarkeit des bevorzugten Habitats entlang der Route. Diese Studie ist die erste, welche die Energiereserven und Flugreichweiten einer Gruppe nah verwandter ziehender Singvogelarten im Asiatisch-Australasiatischen Zugwegssystem untersucht.

86 Introduction

87 Bird migration is a fascinating phenomenon undertaken by billions of birds travelling up to tens of thousands of
88 kilometres between their breeding areas and wintering grounds twice a year (e.g., Hahn et al. 2009; Egevang et
89 al. 2010; Bairlein et al. 2012; Doren and Horton 2018). For landbirds, these global movements concentrate
90 along three major flyways: the Nearctic, the Palaearctic-African, and the Asian-Australasian flyway, respectively
91 (Newton et al. 2008). The miniaturisation of tracking devices, such as satellite transmitters and light-level
92 geolocators, has led to an explosion of tracking studies which has revolutionised our understanding of when
93 and along which routes birds migrate, and where they overwinter (for reviews see e.g. Newton et al. 2008;
94 Fiedler 2009; Bridge et al. 2011; 2013; Finch et al. 2017; McKinnon and Love 2018). Although there are many
95 studies that have investigated the movement ecology of migratory birds along the Asian-Australasian flyway,
96 including storks (Shimazaki et al. 2004; Higuchi 2012), raptors (Higuchi 2012), cranes (Higuchi et al. 2004),
97 waders (Takekawa et al. 2010; Reid et al. 2013; Bellio et al. 2017), gulls (Guo-Gang et al. 2014), and songbirds
98 (Koike et al. 2016; Yamaura et al. 2017; Heim et al. 2018a), the knowledge with respect to how songbirds
99 behave at stopover sites (locations where they rest and fuel between their migratory flight bouts) has
100 increased only slowly along this flyway. Although many field studies have significantly contributed to this
101 research area (e.g., Valchuk et al. 2005; Wang et al. 2006; Biserov and Medvedeva 2009; Fukai et al. 2010; Nam
102 et al. 2011; Leliukhina and Valchuk 2012; Yong et al. 2015, 1998; Sander et al. 2017; Senda et al. 2018; Bozó et
103 al. 2018a; Heim et al. 2018b), there is still a strong bias in terms of number of studies and therefore general
104 knowledge of songbirds' stopover ecology towards the Nearctic and the Palaearctic-African flyway. Since
105 songbird migrants spend far more time and energy during stopover than during migratory flights (Wikelski et al.
106 2003; Schmaljohann et al. 2012), we can learn from stopover ecology studies how songbirds organise their
107 migratory journey in terms of these two currencies, reviewed e.g. by Alerstam (2011), but little is known about
108 this for the Asian-Australasian flyway (Wang et al. 2006; Yong et al. 2015). To address this gap, we analysed
109 ringing data of ten closely related warbler species of the genus *Phylloscopus*, *Arundinax*, *Acrocephalus*, and
110 *Locustella* captured by mist-nets at a favourable stopover site at the southern border of their breeding range in
111 the Russian Far East during autumn migration.

The first objective of this study was to describe the amount and variation of energy stores between the species. If biologically relevant differences were found this would potentially indicate differences in the general movement ecology of the species (cf. Schaub and Jenni 2001; Stępniewska et al. 2018). For the Palaearctic-African flyway it has been shown, e.g. that three songbird migrants (Eurasian Reed Warbler *Acrocephalus scirpaceus*, Sedge Warbler *A. schoenobaenus*, and Garden Warbler *Sylvia borin*) differed in their amount of energy stores, rates of accumulating energy, and stopover durations in autumn (Schaub and Jenni 2001). It was argued that Reed Warblers make use of low, but predictable, food resources which would yield low rates of accumulating energy and thus explain the generally long stopover durations (Schaub and Jenni 2001). Stopover durations were more variable in the closely related Sedge Warbler, probably because this species strongly relies on its preferred diet (reed aphids) which is spatially and temporally unpredictable, but can be superabundant (Bibby et al. 1976; Bibby and Green 1981, 1983; Schaub and Jenni 2001). The shortest stopover durations and thus the highest rates of accumulating energy were found in Garden Warblers, which are both probably related to the species' ability to switch between an arthropod and fruit diet (Schaub and Jenni 2001). Thus, if we find differences in the energy stores between species, we can carefully relate these to potential differences in their movement ecology.

The second objective was to assess whether the energy stores generally increase within the day and/or within the season in a between-individual comparison. First, we predict that if birds experience favourable feeding conditions at the stopover site, they will generally accumulate energy stores within the day (Delingat et al. 2009). Second, we predict that birds arriving late in season will have higher energy stores than birds captured early in the season probably to increase migration speed (Fransson 1998; Dänhardt and Lindström 2001).

The third objective was to estimate the potential flight range of the species based on the energy stores at capture, the generally prevailing wind conditions, and the average night length (cf. Sander et al. 2017). Potential flight ranges were restricted to the night, because all species are most likely nocturnal migrants (Wang et al. 2019) and cf. Hansen (1954) and Dorka (1966) for closely related European species. With the third objective, we intend to provide the first estimates of the average distance potentially covered per nocturnal flight bout for the considered species along the flyway. The results on all three objectives will substantially

improve our understanding on the movement ecology of songbird migrants along the Asian-Australasian flyway.

Materials and Methods

Study site and capture protocols

Birds were caught within the volunteer-based Amur Bird Project at Muraviovka Park in the Russian Far East (49°55′08, 27°′N, 127°40′19,93′′E), cf. Heim and Smirenski (2013). This nature reserve includes wetlands, meadows, and crop fields with small forest islands in the Amur River valley. Birds were trapped daily from local sunrise to sunset during five autumn seasons (August–October 2011–2015). Up to 15 mist-nets (Ecotone, Poland) with single lengths of six, twelve or 18 metres (mesh-size 16 or 30 mm), which added up to a total length of maximal 148 metres, were placed in different habitats along a gradient from the low wetland to the river terrace, including *Artemisia* thickets, willow-shrubs (e.g., *Salix miyabeana*, *S. pierotii*), forests of young oak (*Quercus mongolica*) and poplar trees (e.g., *Populus tremula*) and a small pine plantation (*Pinus sylvestris*) (for details see Heim et al. 2012, 2018a). We measured wing length (maximum chord) to the nearest 0.5 mm (Svensson 1992) and body mass using an electronic balance to the nearest 0.1 g. We quantified the visible subcutaneous fat on a nine-class scale (0–8, “fat score”; Kaiser 1993) and the size of the pectoralis muscle on a four-class scale (0–3, “muscle score”; Bairlein 1995). After ringing, birds were released immediately.

Energy stores

We compared energy stores rather than body mass, because the ten warbler species differ substantially in their size (range of wing lengths in this study 47–84.5 mm) and body mass increases allometrically with the size of the bird, cf. Labocha and Hayes (2012). We estimated “lean” body mass from wing length using species-specific linear regressions based on “lean” individuals with a fat score of 0 and a muscle score less than 3 of the corresponding species. Birds were caught in the study area in the autumnal migratory seasons as mentioned

above and additionally during three spring seasons (April–June 2013, 2015, and 2016) to increase the respective sample sizes:

$$\text{“lean” body mass}_i [\text{g}] = a * \text{wing length}_i [\text{mm}] + b \quad (1)$$

with a [in g/mm] as the slope and b [in g] as the intercept. In three species (Arctic Warbler *Phylloscopus borealis*, Pale-legged Leaf Warbler *Phylloscopus tenellipes*, and Two-barred Warbler *Phylloscopus plumbeitarsus*), the species-specific sample size of “lean” individuals was below ten. As “lean” body mass was similarly related to wing length across these three species (see Electronic Supplementary Material 1a), we pooled the data of “lean” individuals of these three species, to estimate how a change in wing length affects a change in “lean” body mass. Results of all corresponding linear regressions are given in the Electronic Supplementary Material 1b.

Energy stores were calculated for each individual by considering the species-specific regression analysis to estimate the individual “lean” body mass as:

$$\text{energy stores}_i = (\text{body mass}_i [\text{g}] - \text{“lean” body mass}_i [\text{g}]) / \text{“lean” body mass}_i [\text{g}] \quad (2)$$

Flight range estimation

Flight ranges (Y) were estimated following Delingat et al. (2009) according to the equation:

$$Y_i [\text{km}] = 100 * U [\text{km/h}] * \ln(1 + f_i) \quad (3)$$

with f_i as the individual energy stores _{i} [from equation 2] and U as the generally assumed flight speed [in km/h]. Flight speed is the bird’s speed in relation to the ground and is a function of the bird’s air speed, i.e., its speed relative to the air, and the influence of wind (Liechti 2006). To the best of our knowledge, there are no air speed estimates available for the ten songbird species considered in this study. We therefore applied the average air speed estimate of two congeneric species (Willow Warbler *Phylloscopus trochilus*: 9.5 m/s and Marsh Warbler *Acrocephalus palustris*: 8.8 m/s, cf. Bruderer and Boldt (2001), which is 9.2 m/s (33 km/h), as an approximate estimate for all species.

The influence of wind can be negative (head winds) or positive (tail winds) and is further influenced by side wind (Kemp et al. 2012a). To account for the prevailing wind conditions and their effect on the flight range estimates, we estimated the general wind conditions, i.e., flow assistance, at the study site towards the wintering ground using the National Centres for Environmental Prediction Reanalysis II data from the National Oceanic and Atmospheric Administration (NOAA, Boulder, CO, USA; <http://www.cdc.noaa.gov/cdc/data.ncep.reanalysis.derived.html> (Kalnay et al. 1996). Wind data were obtained via the R package “RNCEP” (Kemp et al. 2012b) and were shown to correlate well with real wind measurements (Bromwich and Wang, 2005; Chelton and Freilich, 2005; Schmaljohann et al., 2009, 2011). The influence of wind was quantified using equation^{Airpseed} and following Kemp et al. (2012a):

$$flow\ assistance\ \left[\frac{m}{s}\right] = flow\ speed\ \left[\frac{m}{s}\right] * \cos(\theta) + \sqrt{z^2 - (y * \sin(\theta))^2} - z \quad (4)$$

with θ is the angular difference between the direction into which the wind is blowing and the bird’s migratory direction towards its general wintering ground. The latter was estimated by calculating the average centres of the wintering ranges for each species; data were derived from the IUCN range maps (BirdLife International 2017). Species’ average centre of the wintering range was simplified as the mean of the northernmost and southernmost latitude and the eastern- and westernmost longitude. Since the wintering ranges of the ten species coincide to a large extent (varying only from 25°–5° N and 113°–91° E; BirdLife International 2017, the preferred migratory direction of all study species was set to the overall corresponding mean value, i.e. 14° N and 104° E. z is bird’s speed [in m/s] relative to the wind. y is wind speed [in m/s]. We applied the “NCEP.flight” function of the R package “RNCEP” (Kemp et al. 2012a) with “flow.assist” set to “NCEP.Airspeed”, “air speed” set to 9.2 m/s (see above) and “path” to “great circle”. As all ten warbler species probably migrate exclusively during the night (Wang et al. 2019), flow assistance was estimated for the average night length the birds experienced during the field study, which was eleven hours. The assumption that the warblers migrated only during the night seems reasonable, because most songbirds setting off with high energy stores and towards the seasonally appropriate migratory direction start their migratory flight bout shortly after sunset (Müller et al. 2016, 2018) and terminate it shortly before sunrise (Liechti et al. 2018). Thus, “hours” was set to 11 and “evaluation.interval” to 220 min (3 downloads per night).

For further analyses, we obtained the best flow assistance of four different pressure levels (1000, 925, 850, and 700 mbar) (cf. Liechti 2006; Schmaljohann et al. 2009; Mateos-Rodríguez and Liechti 2012), a bird could have potentially experienced towards the assumed centre of the wintering range during each evaluation interval, since many songbird species depart from stopover when wind conditions, i.e. flow assistance, are favourable (reviewed in Liechti 2006; Shamoun-Baranes et al. 2017). We calculated the mean of these three flow assistance estimates per night, so that we obtained one average value per night. Visual inspection of these values did not show any trend of flow assistance with day of year (see Electronic Supplementary Material 2). Therefore, we considered the 75%-quartile, i.e. the best 25 % of these values, of flow assistance to capture the probable wind conditions the ten warbler species experienced during their potential nocturnal migratory flight when “departing” from the study site. Although this is of course a simplification, this approach seems feasible, because songbirds are known to generally time their departure from stopover to coincide with favourable wind conditions (Dierschke and Delingat 2001; Erni et al. 2002; Schmaljohann et al. 2017) and also adjust their flight altitude to these (Schmaljohann et al. 2009; Shamoun-Baranes et al. 2017). Most of the studied warbler species were found to migrate mostly with favourable winds at our study site (Bozó et al. 2018a). Negative flight range estimates were set to zero.

Migration distance was defined as the great circle distance between the location of the study site and the centre of the wintering range (based on BirdLife International 2017 range maps, see Electronic Supplementary Material 3). To estimate the potential number of stopovers required to reach the latter, we neglected the geographical differences of the species’ winter distribution and assumed furthermore that the birds would always resume migration with the same energy stores and would not continue their flight into the day time. This assumption, i.e., the level of refuelling is similar at each stop over site, seems reasonable because birds do not have to cross major ecological barriers, such as mountains, deserts, and/or the sea, but migrate across benign habitats towards their migratory destination. It, thus, seems rational that the common migration strategy of these migrant birds can be described as performing alternating cycles of accumulating relatively low energy stores during stopover and flying for a single night.

239 *Statistical analyses*

240 Statistical analyses were performed using the R 3.4.2 statistical software package (R Core Team). Day of capture
241 was transformed to day of year (1 = 1 January).

242 Variation in energy stores between species was modelled using a linear mixed effect model (LMM)
243 assuming normally distributed errors. “Species” was included as the explanatory variable. “Year” was included
244 as a random factor (intercept) to account for potential differences between the years.

245 Variation in energy stores within the day was modelled separately for each species using a LMM
246 assuming normally distributed errors. Each model included “hours after sunrise” as the explanatory variable.
247 “Year” was included as a random factor (intercept), see above.

248 Variation in energy stores within the season was modelled separately for each species using a LMM
249 assuming normally distributed errors. Each model included “day of year” as the explanatory variable. “Year”
250 was included as a random factor (intercept), see above.

251 Residual analyses of all models did not show any violation of model assumptions. To assess
252 uncertainty of the model estimates and model predictions, we used Bayesian methods to obtain uncertainty
253 estimates of the model parameters (Korner-Nievergelt et al. 2015). We used improper prior distributions,
254 namely $p(\beta) \sim 1$ for the coefficients and $p(\sigma) \sim 1/\sigma$ for the variance parameters in all models, following Korner-
255 Nievergelt et al. (2015). To obtain posterior distributions of the respective models, we directly simulated 5000
256 values from the joint posterior distributions of each model’s parameters applying the function “sim()” of the R-
257 package “arm” (Gelman and Hill 2007). We used the means of the simulated values from the joint posterior
258 distributions of each model’s parameters as the respective model estimates, and the 2.5% and 97.5% quantiles
259 as limits for the 95% credible intervals (CrI), following Korner-Nievergelt et al. (2015). We declare an effect to
260 be significant if the corresponding 95% CrI does not include zero or if the 95% CrIs of the comparing groups do
261 not overlap.

262

263 **Results**

In total, 5,948 individuals were included in this study. Each species was caught in each year during the study period. With 120 individuals the Pale-legged Leaf Warbler was the rarest and with 2,125 individuals the Yellow-browed Warbler *Phylloscopus inornatus* was the most abundant species during the autumn seasons in 2011–2015 (for sample sizes for all species see Fig. 1).

Variation in energy stores between species

Energy stores were found to differ significantly between the ten study species (Figs. 1). The energy stores were highest in the Pallas's Leaf Warbler *Phylloscopus proregulus*, with a mean of 0.097 (95% CrI: 0.086, 0.108) and lowest in the Two-barred Warbler, with a mean of -0.003 (95% CrI: -0.018, 0.11). According to the distribution of the 95% CrIs of the species' energy stores (Fig. 1), the Two-barred Warbler did not have significantly different energy stores than the Black-browed Reed Warbler *Acrocephalus bistrigiceps* and the Thick-billed Warbler *Arundinax aedon*, while the energy stores of the remaining species were all significantly higher than in the Two-barred Warbler. In addition, the Arctic Warbler had significantly higher energy stores than the Black-browed Reed Warbler, the Thick-billed Warbler, the Yellow-browed Warbler, and the Radde's Warbler *Phylloscopus schwarzi*, but significantly lower energy stores than the Pallas's Leaf Warbler (Fig. 1).

Variation in energy stores within the day

At sunrise, birds were generally in lean body condition, cf. Tab. 1, Fig. 2. Energy stores significantly increased within the day in all species (Tab. 1, Fig. 2). The strongest increase was found in Pallas's Leaf Warblers, which increased their energy stores from 0.8 % to 4.4 % of the bird's "lean" body mass (0.011 h^{-1} , 95% CrI: 0.010 h^{-1} , 0.013 h^{-1}) within the day, and in Pale-legged Leaf Warblers (0.011 h^{-1} , 95% CrI: 0.007 h^{-1} , 0.014 h^{-1}). The lowest increase was found in Pallas's Grasshopper Warbler *Locustella certhiola* (0.005 h^{-1} , 95% CrI: 0.003 h^{-1} , 0.007 h^{-1}), Black-browed Reed Warbler (0.006 h^{-1} , 95% CrI: 0.004 h^{-1} , 0.008 h^{-1}), and Radde's Warbler (0.005 h^{-1} , 95% CrI: 0.002 h^{-1} , 0.008 h^{-1}) (Tab. 1, Fig. 2).

Variation in energy stores within the season

At the beginning of the autumnal migration season, birds were in rather lean condition, as expressed by the low energy stores (Tab. 2, Fig. 3). For all but two, the Arctic Warbler and Two-barred Warbler, energy stores at capture significantly increased between individuals within the season and varied from 0.0006 to 0.0024 per day (Tab. 2, Fig. 3). The strongest increase was found in the Radde's Warbler (0.0024 day^{-1} , 95% CrI: 0.0013 day^{-1} , 0.0034 day^{-1}), which showed an increase of 1.1 % of bird's "lean" body mass within 54 days (difference of day of first capture and day of last capture considering all years), and the Pale-legged Leaf Warbler (0.0023 day^{-1} , 95% CrI: 0.0006 day^{-1} , 0.0038 day^{-1}), which showed an increase of 0.9 % of bird's "lean" body mass within 34 days. The lowest increase was found in the Dusky Warbler *Phylloscopus fuscatus* (0.0006 day^{-1} , 95% CrI: 0.0003 day^{-1} , 0.0008 day^{-1}) with an increase of 0.5 % of bird's "lean" body mass within 71 days (Tab. 2, Fig. 3).

Potential flight range

Potential flight range of all individuals of all species captured at the study site varied from 0 to 1,300 km (Fig. 4). The median potential flight ranges per species varied from 0 to 360 km. The former belongs to the Two-barred Warbler (25% and 75%-quantile: 0 and 120 km), while the latter belongs to the Pallas's Leaf Warbler (25% and 75%-quantile: 205 and 530 km). A certain proportion of each species (highest in Pallas's Leaf Warbler with 32 % of captured individuals) would have been able to fly for the entire night (10 hours) and to cover a distance of more than 470 km in one flight bout (Fig. 4). These birds would have to stop approximately nine times (considering a migration distance of ~ 4,000 km, BirdLife International 2017) during autumn migration to reach their assumed centre of the wintering range.

Discussion

Our study clearly demonstrates that the ten warbler species significantly differed in their energy stores at capture at our stopover site in the Russian Far East (Fig. 1). Assuming that the between-individual effects quantified in our approach (Figs. 2, 3) agree with the effects acting at the individual level, we further found that

the species varied significantly in their degree of change in energy stores over time, i.e., within the day and within the season (Figs. 2, 3). The Pallas's Leaf Warblers carried the highest energy stores and had the strongest increase in energy stores within the day and within the season (Figs. 1 – 3). The Two-barred Warbler, in contrast, had low energy stores and these were hardly affected by time of the day and day of the year (Figs. 1 – 3). This strongly suggests that there are probably significant differences in the stopover ecology between the species, with Pallas's Leaf Warbler being probably able to switch to more commonly food sources, while the Two-barred Warbler and Pallas's Grasshopper Warbler are probably more stenoeicous species (cf. Schaub and Jenni 2001; Stępniewska et al. 2018).

Variation in energy stores between species

The significant species-specific differences in the energy stores are probably related to specific habitat requirements and/or migration strategies. Although all considered species are mainly insectivorous, the study site may offer species-specific refuelling conditions, because some species may have a broad or narrow niche concerning the habitats in which they forage during stopover. Previous work found supportive evidence for this assumption and detailed that some warblers occur in many different habitats at our study site, while others seem to be more specialised (Bozó et al. 2018b). The majority of Pallas's Leaf Warblers was captured in deciduous forest, pine forest, and shrubs. As this species showed the highest energy stores of all warbler species, we carefully argue that the potential of exploiting different habitats may be one reason why the species showed high energy stores (Tab. 1, Figs. 1) and increased these within the day and within the season so strongly (Tabs. 1, 2, Figs. 2, 3). The Thick-billed Warbler is known to forage in reeds and willow shrubs close to water (del Hoyo and Christie 2006). However, its abundance was not related to a certain habitat type at our study site (Bozó et al. 2018b), which may indicate that the species feeds in a high variety of different habitats during migration. Despite this, energy stores and their changes within the day and within the season were not especially pronounced (Tabs. 1, 2, Figs. 1 - 3). The Pallas's Grasshopper Warbler and the Black-browed Reed Warbler, in contrast, were only abundant in the reeds (Bozó et al. 2018b) and had relatively low energy stores (Tab. 1, Fig. 1). Although the range and types of habitats used during stopover may be indicative for the more general pattern in energy store change over time, i.e. day and season, there are other factors, e.g., the

potential of exploiting a variety of food resources, explaining the variation in energy stores between the species and over time which we did not cover in this study. In summary, we assume a combination of multiple factors (the potential of exploiting different habitats, differences in the refuelling strategy according to the distribution of species-specific refuelling habitats along the migratory route, the potential of exploiting a variety of food resources) jointly shape variation in energy stores between the species.

We therefore assume that the between-species differences in energy stores and change over time may also result from species-specific refuelling strategies. The variety of habitats which could be potentially exploited for refuelling and their distribution along the migratory route may determine to which extent the species refuel at a given stopover site (Schaub and Jenni 2001). Species refuelling to a larger extent (i.e. Pallas's Leaf Warbler; Tabs. 1, 2, Figs. 1 - 3) may increase the distance covered by the next flight bout because they might be more restricted to certain habitat types (e.g., Pallas's Leaf Warbler, forest and shrubs) than others (e.g. Thick-billed Warbler, Radde's Warbler) (Bozó et al. 2018b).

The degree of food-specialisation, and thus if they are more opportunistic than others, may also determine species' migration strategy. The variety of food resources the species can use (insects only or insects and fruits) and the ability to switch between these related to their abundance may influence refuelling patterns (Schaub and Jenni 2001). In contrast to the Leaf Warblers, Grasshopper and Reed Warblers are both able to include vegetable material into their diet (del Hoyo and Christie 2006), which means, they are more variable in their foraging habits and may have more predictable resources. Pallas's Leaf Warblers and Arctic Warblers prey on insects (high energy stores, Fig. 1) whereas Black-browed Reed Warblers, Pallas's and Grasshopper Warblers (and possibly Black-browed Reed Warblers as well) include vegetable material into their diet during migration (Dement'ev and Gladkov 1954) (low energy stores, Fig. 1). Since very little information is available on food requirements of the studied taxa during stopover, it is difficult to assess how variation in food requirements may affect their migration strategy along the Asian-Australasian flyway.

Relating these findings to the refuelling patterns of different warblers discussed in Schaub and Jenni (2001), we conclude that Pallas's Leaf Warblers might depend more strongly on the presence of specific habitats, which they find and further exploit at a higher rate at our study site (Fig. 2). Other species, such as the

Thick-billed Warbler and the Radde's Warbler, may find suitable stopover sites more regularly along the route, as they are found to be more generalistic.

The estimates of energy stores differ from the true values because the individual lean body mass was approximated by the bird's wing length only but not individually measured for each bird, cf. Guglielmo et al. (2011). Furthermore, migratory birds may reversible fasten below their lean body mass (Salewski et al. 2010), so that the measured/estimated lean body mass differs from the true value. Both issues may over- and underestimate the energy stores. In addition, mist-netting data is probably biased towards lean birds because foraging activity is condition-related resulting in a higher probability of catching the more mobile individuals. The generally low energy stores (Fig. 1) maybe a specific phenomenon of our study site where birds do not encounter any major ecological barrier before and after stopping there and thus do not have the urge to accumulate high amounts of energy.

Variation in energy stores within the day

Many migratory songbirds perform a stop-and-go strategy (Åkesson and Hedenström 2007) and build up energy stores during the day (Delingat et al. 2009), while migrating in the night (Dorka 1966; Müller et al. 2016). With the between-individual approach in our study we intended to approximate the within-individual effects of time of day on the energy stores. (Delingat et al. 2009) have shown that the first-traps-by-time-of-day-method (linear relationship between body mass and time of day) may not always be applicable to describe the individual increase in energy stores in migrating birds during stopover. They have also shown that, especially in low-sized samples, an increase in body mass within the day is rarely found in a between-individual approach. Despite this, we found such an effect in all species (Tab. 1, Fig. 2). If our between-individual approach correctly reflects the individual increase in energy stores within the day, birds build up more energy stores than they lose during the night. This indicates that the study site is an important refuelling area highlighting its significant status for conservation. Differences in the degree of refuelling (increase in energy stores, Tabs. 1, 2, Figs. 2, 3) may be related to the species-specific foraging habitat (see above), but species of the same foraging habitat (del Hoyo and Christie 2006; Glutz von Blotzheim and Bauer 1991) did not always

have a similar increase of energy stores within the day (Fig. 3). The Pallas's Leaf Warbler forages in the canopy and was found to have the strongest increase, while the Pale-legged Leaf Warbler, which was also found to have a strong increase, forages closer to the ground, similar to the Radde's Warbler, which had the lowest increase of energy stores within the day. The mechanisms of refuelling in these small migratory passerines, and whether they are able to switch the preferred diet in relation to abundance of food, remain unknown. With our study, we have provided the first descriptive results which can be compared with patterns found in prospective studies on these species and in this region.

Variation in energy stores within the season

The variation in energy stores within the day was stronger than the seasonal and the variation explained by hours after sunrise was greater than that explained by day of the year (Tab. 1, 2, Fig. 2, 3). Nevertheless, we found an increase in energy stores and thus increasing flight ranges within the season in eight species (Tab. 2, Fig. 3). Similar patterns were found in e.g. Garden Warblers *Sylvia borin* and Northern Wheatears *Oenanthe oenanthe* (Bairlein 1998; Corman et al. 2014), and other songbird species migrating along the Asian-Australasian flyway, such as the Red-flanked Bluetail *Tarsiger cyanurus* (Wang et al. 2006) and *Luscinia* thrushes (Biserov and Medvedeva 2009). The between-individual increase in energy stores within the season agrees with the idea that birds tend to maximise migration speed when being late in season (Fransson 1998). Birds are thought to exploit favourable refuelling sites more intensively, leading to high rates of energy accumulation and thus high migration speeds (cf. Alerstam and Lindström 1990; Lindstrom and Alerstam 1992). Speeding up migration may allow birds to counterbalance the upcoming seasonal temperature decrease and hence diminishing insectivorous food sources within the season, and the increasing competition for habitats at the wintering grounds, at least for species that defend territories there.

Potential flight range

In eight of our studied species, birds with the highest energy stores would have been able to fly throughout the whole night (Fig. 4). Such high energy stores could indicate that they cover relatively long distances during the

nocturnal migratory flight bout, and thus minimise the number of stopovers required to reach the wintering range. In the Pallas's Leaf Warbler, birds with high energy stores (75%-quantile, Fig. 4) could cover a distance of over 500 km in one flight bout and thus might have energy stores left after the nocturnal flight. This could be interpreted as a margin of safety in case of unfavourable weather and/or feeding conditions at the next stopover site (Moore and Aborn 1996). Birds having lower energy stores than required for a whole night-time flight (Two-barred Warbler, Black-browed Reed Warbler, Fig. 4) either will depart with lower energy stores from the current stopover site to search for better refuelling opportunities in the surroundings, so called "landscape movements", or are not in the condition for departure and thus stay and prolong their stopover duration until sufficient energy is stored, reviewed in Schmaljohann and Eikenaar (2017).

Conclusion

This explorative investigation on ten conspecific small long-distance migrants fills an imminent knowledge gap concerning the refuelling patterns at a stopover site along the Asian-Australasian flyway. Even though the underlying mechanisms of the movement ecology of the species found at the study site are still unknown, we found significant differences in their energy stores suggesting that they differ in their ability to exploit the stopover site, or that they perform different refuelling strategies. Studying how birds organise their migration along the Asian-Australasian flyway is important, as migrant birds along this flyway are showing declining trends (Yong et al. 2015), and the conditions are deteriorating due to urbanisation and industrialisation (Alauddin and Quiggin 2008), increasing agriculture intensification, climate change and unsustainable harvest (Edenius et al. 2017; Kamp et al. 2015). Research on migration routes and stopover sites is of imminent conservation concern, as suitable stopover habitats to rest and forage are crucial for the successful connection between wintering and breeding ranges and furthermore for the protection of migratory species (Kirby et al. 2008).

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631 Figures

632 Fig. 1: Estimated average energy stores of each species (sample sizes are given above species abbreviation) with 95%
633 credible intervals. Dotted lines indicate which species differ significantly in their energy stores from each other.

634 Abbreviations: tbw – Two-barred Warbler, bbrw – Black-browed Reed Warbler, thbw – Thick-billed Warbler, ybw – Yellow-
635 browed Warbler, rw – Radde’s Warbler, pgw – Pallas’s Grasshopper Warbler, dw – Dusky Warbler, pllw – Pale-legged Leaf
636 Warbler, aw – Arctic Warbler, plw – Pallas’s Leaf Warbler.

637 Fig. 2: Increase in energy stores with hours after sunrise by “first-traps-by-time-of-day-method” modelled with linear mixed
638 effect models separately for each species, the feasibility of this approach is addressed in the discussion and see also
639 Delingat et al. (2009). Species-specific regressions are given as the black solid line and the corresponding 95% credible
640 intervals are given in grey, when the effect was significant. Results of the appropriate linear mixed effect models are
641 provided in Tab. 1.

642 Fig. 3: Increase in energy stores within the season (day of the year) modelled with linear mixed effect models for each
643 species. Species-specific regressions are given as the black solid line and the corresponding 95% credible intervals are given
644 in grey, when the effect was significant. Results of the appropriate linear mixed effect models are provided in Tab. 2.

645 Fig. 4: Estimated flight ranges of each species. Boxplots show the 5, 25, 50, 75 and 95 % percentiles as well as outliers
646 (dots). Significant differences between the groups are graphically illustrated by the non-overlapping “notches”. Grey line
647 shows the maximal distance (470 km) birds could cover during one migratory flight bout (with average length of night: 11
648 hours, for details see methods). For abbreviations see Fig. 1.